SPAWNING AND EGG PRODUCTION OF OYSTERS AND CLAMS

H. C. DAVIS AND P. E. CHANLEY

U. S. Fish and Wildlife Service, Milford, Conn.

Many aspects of the physiology of reproduction of oysters and clams have been investigated, and most investigators have been impressed by the great number of eggs produced by these animals. Although the number of eggs released, by individual females during a season, is an important factor in determining what constitutes a sufficient breeding stock, this number had never been determined experimentally, and estimates of the number have varied widely.

Brooks (1880) was the first to estimate the number of eggs produced by a female American oyster, *Crassostrea virginica*. His estimate was based on the volume of eggs washed out of ripe females and the calculated volume of a single egg. From the volume calculation Brooks' figures gave 18,750,000 to 125,000,000 eggs, but he believed that as much as 50 per cent should be allowed for foreign matter washed out with the eggs. His estimate, therefore, was nine million eggs per female but states that "an unusually large oyster" gave an estimated 60 million eggs. Churchill (1920) estimated over 16 million eggs and Nelson (1921) estimated 16 to 60 million eggs per female. Galtsoff (1930) observed that individual oysters may release 15 million to 114.8 million eggs at a single spawning and estimated that the maximum number released by a single female during a season may be close to half a billion. Burkenroad (1947), although offering no experimental data, apparently believed Galtsoff's estimate was some ten times too high.

The only known estimate of the number of eggs released by a female clam, *Venus mercenaria*, is that of Belding (1912) who merely states in his summary that the average number of eggs for a $2\frac{1}{2}$ -inch quahaug is about two million.

The experiments we are reporting were designed to determine the total number of eggs actually produced by individual oysters and clams under experimental conditions, and to find whether there was any correlation between the size of the individual and the number of eggs produced. We also hoped to find whether this total was affected by the time interval between spawnings, or by the number of times the female spawned.

For our first experiment, 75 oysters were brought into the laboratory on December 30, 1954, and placed in conditioning trays of running sea water at 10.0° – 13.0° C. The temperature of the sea water in the trays was raised to 20.0° – 21.0° C. on the 31st of December. The clams were obtained on January 5, 1955 and 75 individuals were placed in running sea water at 18.0° – 19.0° C. (Loosanoff and Davis, 1950).

In mid-January, after approximately two weeks at conditioning temperature, we started spawning 25 of the clams and 25 of the oysters at three-day intervals. A second group of 25 oysters was spawned at five-day intervals and a third group of 25, at intervals of seven days. The second group of 25 clams was spawned at in-

tervals of seven days and the third group of 25 clams, at intervals of 14 days. To determine the number of eggs produced by each female, each individual was placed in a separate spawning dish, and the shells of the females were marked with a sex symbol and an individual number. The males were discarded as soon as they were identified. The number of eggs released by each female was determined and recorded each time she spawned (Tables I through VI).

The spawning records of the oysters subjected to spawning stimuli every three days are shown in Table I. Within this group the total number of eggs per female ranged from 7.8 million to 59.9 million, while the number released at a single spawn-

-														
Days after]	Female :	number						
spawning	1	2	3	4	5	6	7	8	9	10	11	12	13	14
$\begin{array}{c} 0\\ 0\\ 3\\ 6\\ 9\\ 12\\ 15\\ 18\\ 21\\ 24\\ 27\\ 30\\ 33\\ 36\\ 39\\ 42\\ 45\\ 48\\ 51\\ 54\\ 57\\ 60\\ 63\\ 61\\ 61\\ 64\\ 64\\ 64\\ 64\\ 64\\ 64\\ 64\\ 64\\ 64\\ 64$	9.0 1.0 3.1 2.8 	2.0 0.8 8.4 18.7 5.8 9.6 9.6 9.4 5.2 5.2 0.03	6.8 	7.9 3.8 6.9 1.6 4.7 3.5 3.7 3.7	6.3 8.7 16.3 10.1 	0.4 0.5 	<0.1 2.0 6.8 3.3 7.7 - - 9.7 7.0 - - 3.5 - - - - - - - - - - - - - - - - - - -		<0.1 	$\begin{array}{c} - \\ - \\ - \\ 0.1 \\ 0.1 \\ 4.0 \\ 9.2 \\ 6.5 \\ 5.6 \\ 4.1 \\ 4.0 \\ 2.8 \\ - \\ 5.9 \\ 3.6 \\ 2.0 \\ 2.4 \\ - \\ - \\ 2.7 \\ 0.6 \\ 0.2 \\ - \\ - \\ - \\ - \\ - \\ - \\ - \\ - \\ - \\ $				8.4
Total eggs	29.8	59.9	11.0	32.1	41.4	7.8	40.0	25.7	34.4	53.7	43.1	22.2	29.0	10.5

 TABLE I

 Number of eggs (in millions) released by individual female oysters induced to spawn at 3-day intervals

ing ranged up to 28.3 million. The number of spawnings per female ranged from two to 16. Only number 14 failed to spawn on two or more consecutive three-day trials, and number 10 spawned repeatedly at three-day intervals. The highest number of eggs (59.9 million) was produced by a female that spawned nine times. The female that spawned 16 times ranked second, and a female that spawned only five times ranked third. The lowest total number of eggs was released by a female that spawned seven times. Tables II and III show similar data for the groups spawned at five- and seven-day intervals.

The record for clams spawned every three days (Table IV) shows a range from 17.1 to 37.4 million in the total number of eggs released. The highest number released by any female in this group at a single spawning was 17.7 million. The num-

118

Days after		Female number													
spawning	1	2	3	4	5	6	7	8	9	10	11	12	13	14	
0	0.7	0.7	$\frac{1}{0}$		_			_					_		
10	3.4		1.2	1.6	1.0	6.8	7.0	3.4	0.1			_			
20	10.0	_		3.1			_	8.4	9.5	10.1	7.0		-	_	
30	11.8	32.8	10.6	9.1	1.9	15.5	12.6	8.4	6.6	$\frac{10.1}{-}$		2.6	35.6	9.3	
40 45	7.4		16.1	1.8	0.0					9.2	_	_		-	
50	$\frac{1.3}{-}$	- 1.2	1.2					0.3	1.2	4.3		- 1		10.9	
60 65		4.2			_	2.3			0.3		_	0.8	_	10.8	
70 75	0.9	< 0.4	< 0.1							0.2		< 0.1	_	_	
75 T- (-1	0.1			10.7		25.2									
lotal eggs	42.0	52.2	46.6	19.7	11.9	35.3	20.3	27.7	28.3	23.8	7.0	12.5	40.0	20.1	

 TABLE II

 Number of eggs (in millions) released by individual oysters induced to spawn at 5-day intervals

ber of spawnings per female ranged from three to 10, and the female producing the highest total number of eggs spawned seven times. Second highest total was by a female spawning nine times, and the third ranking female spawned only three times. The lowest total was by a female that spawned five times. Tables V and VI give similar data for the clams spawned at seven-day and at 14-day intervals.

The three groups of oysters, spawned at different intervals, were compared after arranging the females according to their rank in egg production (Table VII). The range in total number of eggs per female was from 10 thousand to 66.4 million.

TABLE III

Number of eggs (in millions) released by individual oysters induced to spawn at 7-day intervals

		-													
Days after initial	Female number														
spawn- ing	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
0	0.9	0.8	0.2	_						_			_		
7 1	0.8	0.4		12.6											
14	21.0	22.2	5.4	10.1	22.0	0.5	0.3	0.2	0.7	0.4					
21							3.1		—	1.0	1.4	7.7	0.4		
28	19.4	39.0			5.7	—		23.4	8.6		14.2				_
35	7.7	1.6	10.3				17.0		2.5	8.4	25.2		9.0	0.5	
42	1.8	1.9	0.9	4.0		48.8	_			0.7	6.2	12.2	1.4		0.01
49	0.6			< 0.1				13.8							
56	-	0.5	_		0.6	3.3					3.2		_		
63	< 0.1				< 0.1	—	—				0.1	-			
70		—						_			_				—
Total															
ogga	52.2	66.4	16.9	26 7	20.2	52.6	20.4	27 1	110	10.5	50.2	10.0	10.0	0.5	0.01
eggs	52.2	00.4	10.8	20.7	28.3	52.0	20.4	57.4	11.8	10.5	50.5	19.9	10.8	0.5	0.01

TABLE I	V
---------	---

Number of eggs (in millions) released by individual clams induced to spawn at 3-day intervals

Days after					Fe	male num	ber				
initial spawning	1	2	3	4	5	6	7	8	9	10	11
$\begin{array}{c} 0\\ 3\\ 6\\ 9\\ 12\\ 15\\ 18\\ 21\\ 24\\ 27\\ 30\\ 33\\ 36\\ 39\\ 42\\ 45\\ 48\\ 51\\ 54\\ 57\\ 60\\ 63\\ 66\end{array}$	0.3 	7.7 2.1 4.2 3.5 4.2 4.2 4.2		9.3 	4.9 	8.5	13.6 6.4 	5.7 	4.7 		
69				—			0.2			1.5	
Total eggs	18.5	21.7	28.8	21.0	28.1	29.4	37.4	17.1	17.9	25.0	20.1

TABLE V

Number of eggs (in millions) released by individual clams induced to spawn at 7-day intervals

Days after		Female number													
initial spawning	1	2	3	4	5	6	7	8	9	10	11	12	13		
0 7 14 21 28 35 42 49 56 63 70 77 84 91	$\begin{array}{c} 4.1 \\ \hline \\ 3.4 \\ 3.2 \\ \hline \\ 3.1 \\ 2.0 \\ 2.1 \\ 1.4 \\ 0.8 \\ 0.6 \\ \hline \\ 0.8 \\ \hline \\ 0.8 \\ \hline \end{array}$	$\begin{array}{c} 2.0\\ 17.8\\ 0.5\\ 5.7\\ 0.7\\ 4.4\\ 1.7\\ 1.5\\ 0.9\\ 0.4\\ \hline 0.1\\ \hline \end{array}$	$\begin{array}{c} 3.5 \\ 5.2 \\ 2.7 \\ 0.2 \\ 7.2 \\ 0.7 \\ 1.6 \\ 1.9 \\ - \\ 1.0 \\ - \\ 0.2 \\ - \end{array}$	$\begin{array}{c} 2.8 \\ \hline 4.2 \\ 4.4 \\ 1.5 \\ 2.7 \\ 3.0 \\ 1.6 \\ 1.4 \\ 0.7 \\ \hline 0.6 \\ \hline \end{array}$	0.1 	10.2 2.4 3.4 		13.1 2.4 1.7 3.2 0.8 0.3 0.2 —		 2.4 3.3 <0.1 		 12.5 7.5 	 14.7 4.1 1.9 0.2 		
98	0.3	-		—		—	—			-	-	—			
Total egg ^s	21.8	35.7	24.2	22.9	39.5	21.9	22.2	21.7	33.0	8.0	23.4	20.0	20.9		

Days after		Female number													
spawning	1	2	3	4	5	6	7	8	9	10	11	12	13	14	
0	7.0	_				_		_			_		_		
14	2.0	2.8	21.3	10.0	3.3	5.5	20.4	10.5	6.4	2.7					
28	7.7	7.3	3.3	3.5	22.4	8.0	8.8	8.8	13.3	18.5	19.8	24.3	10.5	0.7	
42	3.2	2.7	3.3	5.4	4.2	4.0	4.3	3.2	4.3	1.1		2.7		8.7	
56	1.4	0.5	2.6	1.6	2.2	1.6	1.3	2.0	1.5	8.0	9.3	9.1	3.4	1.5	
70	0.2		0.4	0.3	1.1		1.6	1.2	0.4	2.9	0.7	- 1		0.1	
84	_		0.3	< 0.1	0.3			0.6	0.3	1.6	— I			0.2	
98	0.1					0.2	0.1	0.2				< 0.1	1.0		
112										0.5			_		
Total eggs	21.6	13.3	31.2	20.8	33.5	19.3	36.5	26.5	26.2	35.3	29.8	36.1	14.9	11.2	
00															

TABLE VI

Number of eggs (in millions) released by individual clams induced to spawn at 14-day intervals

Despite the relatively great differences between females, however, the range in all three groups is essentially similar, and the mean number of eggs per female in all three groups is approximately the same. The 14th and 15th ranking females, spawned at seven-day intervals, appear to have abnormally low totals. Except that

TABLE VH

	Oyste	rs		Clams							
Rank	3-day spawning interval	5-day spawning interval	7-day spawning interval	Rank	3-day spawning interval	7-day spawning interval	14-day spawning interval				
$ \begin{array}{c} 1\\2\\3\\4\\5\\6\\7\\8\\9\\10\\11\\12\\13\\1.4\\15\end{array} $	59.9 53.6 43.1 41.3 40.0 34.4 32.2 29.8 29.0 25.6 22.2 11.0 10.4 7.8	52.2 46.6 42.0 35.3 28.3 27.7 23.8 20.3 20.1 19.7 12.5 11.9 7.0	66.4 52.6 52.2 50.3 37.4 28.3 26.7 20.4 19.9 16.8 11.8 10.8 10.5 .5 .01	$ \begin{array}{r} 1\\ 2\\ 3\\ 4\\ 5\\ 6\\ 7\\ 8\\ 9\\ 10\\ 11\\ 12\\ 13\\ 14\\ 15\\ \end{array} $	37.3 29.5 28.8 28.2 25.1 21.7 21.0 20.2 18.7 18.0 17.0 	30.5 35.7 33.0 24.2 23.4 22.9 22.2 21.9 21.8 21.7 20.9 20.0 8.0 —	36.5 36.1 35.3 33.5 31.2 29.8 26.5 26.2 21.6 20.8 19.3 14.9 13.3 11.2 —				
Mean	31.4	28.1	27.0	Mean	24.1	24.2	25.4				
Average per spawning	4.4	5.5	7.2	Average per spawning	3.6	3.6	4.7				

Total number of eggs (in millions) discharged by individual oysters spawned at 3-, 5-, or 7-day intervals, and by individual clams spawned at 3-, 7-, or 14-day intervals. In each group the females are ranked according to egg production

Maximum number of eggs from one female at a single spawning 48,780,000 Maximum number of eggs from one female at a single spawning 24,300,000 they were the last to spawn, spawned only once, and released exceptionally few eggs, there seems to be no reason to exclude them.

A similar comparison of the three groups of clams spawned at different intervals (Table VII) shows that they have even more closely comparable ranges, in the total number of eggs per female, than do oysters. The mean numbers of eggs per individual in the three groups of clams are also in closer agreement.

An analysis of variance test confirms the conclusion that varying the spawning interval from three to seven days for oysters and from three to 14 days for clams did not affect the total egg production. We believe that the similarity of variances and the agreement of means further indicate that each group represented an adequate sample of the populations used.

From Table VII we see that the maximum number of eggs released by one female at a single spawning, in either clams or oysters, may be greater than the seasonal total of many other females in the same population. We also note that the average number of eggs per spawning increases progressively, in oysters, as the interval between spawnings is increased. In clams there is no difference between the groups spawned at three- and seven-day intervals, but the average number of eggs per spawning increases slightly as the spawning interval is increased to 14 days.

If we compare clams with oysters, we find that clams are more uniform than oysters in egg production. The average number of eggs per female varied less from group to group (Table VII), and the range in total number of eggs released by different female clams was not so great. Moreover, as shown by the frequency distribution, the number of female clams producing different total numbers of eggs had a fairly normal distribution with a well-defined modal class at 20 to 24.9 million eggs per female, and the arithmetic mean number of eggs per female (24.6) falls within this class. In oysters, by contrast, the distribution was not obviously a normal one, and there is no well-defined modal class near the arithmetic mean (28.8 million). A comparison of the frequencies of individual spawnings in which different numbers of eggs were released also illustrates the greater variability of oysters since, again, the clams have a lesser range and a somewhat better-defined modal class.

The average number of spawnings per oyster decreases progressively as the interval between spawnings increases, while with clams there is little difference among the three groups. An analysis of variance confirms the conclusion that varying the spawning interval for oysters significantly affects the number of times a female oyster will spawn, with those subjected to spawning stimuli at shorter intervals spawning more frequently. The analysis also shows that varying the spawning interval from three to 14 days had no significant effect on the average number of spawnings per individual clam.

To find whether any correlation existed between the size of the female oyster and the number of eggs produced, we chose the volume of the shell cavity as our best criterion of size. The total number of eggs produced, expressed in millions, was then plotted against the volume of the shell cavity in ml. for each female (Fig. 1). In plotting, different symbols were used to differentiate the groups spawned at different intervals. The plot shows that, while the three separate correlations would differ, there is no striking reversal of trend. The data were therefore combined, and one over-all correlation was computed for all oysters in the experiment considered as a single group. The resulting correlation was reasonably good: r was .54 (significant at the .01 level for 41 degrees of freedom), which means that about 30 per cent of the variation in total egg production for oysters could be attributed to the differences in size as denoted by cavity volume.

For clams a similar plot of the number of eggs in millions was made against the shell cavity volume in ml. (Fig. 2). Again, we used different symbols for the groups spawned at different intervals, but the data were combined for computing an over-all correlation. For clams, r was .38 (significant at the .05 level for 36 degrees of freedom), which means that about 15 per cent of the variation in total



FIGURE 1. Scatter diagram showing the total number (in millions) of eggs produced, plotted against the volume (in milliliters) of the shell cavity, for each of 43 oysters. Different symbols are used to differentiate between females spawned at 3-, 5-, and 7-day intervals.

egg production could be attributed to the differences in size of the female clams used in the experiment.

A similar test was made for a correlation between the number of times a female spawned and the total number of eggs produced. The correlation for oysters was .51 (significant at the .05 level). Thus, in general, females that have a large number of eggs to release will spawn at more frequent intervals than females having a lesser total number of eggs. For clams this correlation was only .17, or was not significantly different from zero.

It should be remembered that the oysters and clams used in this experiment were brought into the laboratory in mid-winter and that conditioning, while in

H. C. DAVIS AND P. E. CHANLEY

trays of running sea water, does not provide optimum feeding conditions. Field observations in Long Island Sound have shown that, in some seasons, oysters that go through the winter with relatively little glycogen may increase this reserve by as much as two or three times in the spring before gonad development begins. Moreover, Loosanoff and Nomejko (1951) showed that the average gonad thickness of oysters in Long Island Sound, at the beginning of some spawning seasons, may be almost double that recorded at corresponding periods of other years. Although no measurements of gonad thickness or glycogen content were taken at the



FIGURE 2. Scatter diagram showing the total number (in millions) of eggs produced, plotted against the volume (in milliliters) of the shell cavity, for each of 38 clams. Different symbols are used to differentiate between females spawned at 3-, 7-, and 14-day intervals.

beginning of the experiment, from inspection we believe that the condition of the oysters used in these experiments was below average for oysters of Long Island Sound.

A similar experiment, involving only nine females, was started on June 27, 1955 with oysters that had developed gonads under normal conditions in Long Island Sound. The total number of eggs per female ranged from 23.2 million to 85.8 million, and averaged 54.1 million eggs per female. Thus, both the average number of eggs and the maximum number per female were about 20 million higher than

in the winter experiment. This was, we believe, at least in part, the result of these oysters having built up additional reserves of glycogen during the spring prior to the initiation of gonad development. Even these oysters, however, gave far fewer eggs than the $\frac{1}{2}$ billion per female suggested by Galtsoff (1930).

From the present studies, and from another experiment in which 70,000,000 eggs were released by one female at a single spawning, we are in general agreement with Galtsoff (1930) on the maximum number of eggs a female oyster may release at a single spawning. Galtsoff's estimate of $\frac{1}{2}$ billion eggs as about the maximum number a female oyster might release in a single season was based, in part, on the assumption that a female might release approximately 100 million eggs at each of five or six spawnings during a season. Our experiment indicates that this would be unlikely. For example, the female that gave the highest number of eggs at a single spawning, 48.8 million, spawned on only two other occasions during the experiment, and on each of these occasions released less than four million eggs. Of the 43 female oysters in the experiment, only one released in excess of 10 million eggs at as many as three spawnings.

At the conclusion of the experiment, all the females were opened and the gonad condition, presence of shell injuries, and degree of Polydora and sponge infestations were noted for each female. Statistical analysis does not reveal any effect of shell injuries, or of Polydora and sponge infestations, on the number of eggs produced by a female oyster. Histology indicated that only one female oyster still contained a few eggs, but that all the female clams still retained a few apparently mature eggs (Loosanoff, 1937).

We were surprised to find that it required about $2\frac{1}{2}$ months, or approximately the duration of a normal spawning season, to completely spawn out either oysters or clams, even though they were subjected to spawning stimuli every three days. Moreover, there was almost no difference in the time required at the different spawning intervals used in this experiment.

There were marked differences, however, between clams and oysters in their behavior when subjected to chemical and thermal stimulation in the spawning dishes. Usually 80 per cent to 100 per cent of the oysters opened within 15 or 20 minutes after being placed in the spawning dishes, and normally they remained open until after spawning or until they were disturbed. Records available on 183 of the 227 spawnings of female oysters, included in the present experiment, showed how long each female was open before starting to spawn. This period ranged from one minute to 219 minutes, with an average of 34.2 minutes. Approximately 80 per cent of the spawnings occurred 30 minutes or less after the female opened, about 10 per cent of the spawnings occurred within 31 to 60 minutes, and about 10 per cent of the spawnings occurred over an hour after the female had opened and started pumping.

Clams, on the other hand, were much less predictable. A few opened almost immediately after being put in the spawning dishes, some opened only after several hours, and usually there were a few that remained closed throughout an attempted spawning. Even after opening they frequently closed again for variable lengths of time for no apparent reason. The interval between the time the clams first opened and the time they started spawning was recorded for 208 of the 235 spawnings in this experiment. This interval ranged from less than five minutes to 840

H. C. DAVIS AND P. E. CHANLEY

minutes, with an average of 137 minutes. Moreover, only 35 per cent of the spawnings occurred within one hour after the clams first opened. Both male and female clams have been observed to spawn for a short time, then, while still remaining open, cease spawning for periods of an hour or more, and finally spawn even more heavily than at first. Also, on several occasions both male and female clams that had been open and pumping vigorously for 30 minutes or more started spawning immediately when placed in dishes of fresh, cooler sea water.

		Femal	es			Males							
Female			Days			Male		Days					
number	1 st	2nd	3rd	4th	5th	number	1st	2nd	3rd	4th	5th		
$ \begin{array}{c} 1\\2\\3\\4\\5\\6\\7\\8\\9\\10\\11\\12\\13\\14\\15\\16\\17\\18\\19\\20\\21\\22\\23\\24\end{array} $	x x x x x x x x x x x x x x x x x x x	x x	X X X X X X X X X X X X X X X X X X X	x x		$ \begin{array}{c} 1\\2\\3\\4\\5\\6\\7\\8\\9\\10\\11\\12\\13\\14\\15\\16\\17\\18\\19\\20\\21\\22\\23\\24\end{array} $	X X X X X X X X X X X X X X X X X X X	X X X X X X X X X X X X X X X X X X X	X X X X X X X X X X X X X X X X X X X	x x x x x x x x x x x x x x x x x x x	X X X X X X X X X X X X X X X X X X X		
21			~			25 26	<u> </u>		x x		-		

TABLE VIII Spawning record of male and female oysters subjected to spawning stimuli daily for five consecutive days; x indicates spawning

As noted in Table I, only one of the 14 female oysters failed to spawn two or more consecutive times when subjected to spawning stimuli every third day, and female number 10 spawned repeatedly at three-day intervals. This led us to suspect that at least some female oysters might not show the two- to five-day refractory period that Galtsoff found (1938, 1940). An experiment was therefore designed to determine whether some female oysters might spawn at more frequent intervals.

For this experiment, 50 oysters were brought into the laboratory April 4, 1955, and placed in conditioning trays at 20.0°–21.0° C. Twenty-one days later these oysters were placed in individual spawning dishes, and both chemical and thermal stimulation were used to induce spawning. Seventeen females and 24 males re-

126

sponded on the first day (Table VIII). After spawning, the males and females were washed separately in cold running sea water, and the shell of each was marked with the appropriate sex symbol and an individual number. All males were then returned to one conditioning tray, and all the females to another tray. Those oysters that did not spawn on this first trial were returned to a third tray. Each morning, for five consecutive days, all oysters were subjected to spawning stimuli and a record of the spawning of each individual was kept.

As shown in Table VIII, of the 24 females in the experiment, 14 spawned on two or more consecutive days, eight spawned on three or more consecutive days, five spawned on four or more consecutive days, and three spawned on each of the five days of the experiment. As was to be expected, 25 of the 26 males in the experiment spawned on three or more consecutive days, nine spawned on four or more consecutive days, and eight spawned on each of the five days of the experiment. By the fifth day, however, it was difficult to induce spawning and the spawning of both males and females was light. However, when these oysters were again subjected to spawning stimuli, after remaining undisturbed in the conditioning trays for an additional week, 22 of the 26 males and 18 of the 24 females responded, releasing approximately average amounts of spawn.

From our experiments, we believe that either there is no refractory period for female oysters, such as Galtsoff (1938, 1940) described, or it is less than 24 hours in duration. Our results suggest that both male and female oysters can spawn, upon proper stimulation, any time they have physiologically-ripe sex cells to discharge. Under constant, or closely spaced intervals of stimulation, we believe they may so deplete their supply of physiologically-ripe sex cells that they are unable to release more until additional sex cells have become physiologically mature. Some females, for example, were observed to give fairly typical spawning motions on the fourth and fifth days of the above experiment without releasing any eggs and yet, spawned normally after several additional days of conditioning.

We wish to express our thanks to the Director of Milford Laboratory, Dr. V. L. Loosanoff, who suggested this problem, for his advice throughout the experiments, and to our colleagues, Mrs. Barbara Myers, for the statistical treatment, and Mr. C. A. Nomejko, for the figures.

SUMMARY

1. The total number of eggs released by individual female oysters, *C. virginica*, conditioned in mid-winter, ranged from 10 thousand to 66.4 million, and averaged 28.8 million.

2. Females that developed gonads under natural conditions in early summer released from 23.2 to 85.8 million eggs for an average of 54.1 million eggs per female.

3. In this experiment the highest number of eggs released by a female oyster in a single spawning was 48.8 million, but in a previous experiment one female discharged 70.0 million. Thus, some females release more eggs at a single spawning than other females do in a season.

4. There was no significant difference in the average number of eggs released in a season whether the oysters were spawned at three-, five-, or seven-day intervals.

5. Female oysters that had a large number of eggs to release tended to spawn more frequently than females that had a lesser number.

6. The average number of spawnings per female oyster decreased progressively as the interval between spawnings was increased.

7. The total number of eggs produced showed a correlation of .54 (significant at .01 level) with the size of the female oyster, as indicated by shell cavity volume.

8. No correlation could be found between the number of eggs produced and Polydora or sponge infestation, or shell injury.

9. We find no two- to five-day refractory period during which female oysters cannot be induced to spawn, as reported by earlier investigators.

10. The total number of eggs released by individual female clams, *V. mercenaria*, ranged from eight million to 39.5 million, and averaged 24.6 million per clam.

11. The highest number of eggs released by any female clam at a single spawning was 24.3 million.

12. For clams, the correlation between number of eggs produced and volume of shell cavity was .38 (significant at the .05 level).

13. There was no significant difference in the average number of eggs released in a season whether the clams were spawned at three-, seven-, or 14-day intervals, nor was there any significant difference in the average number of spawnings per female.

14. The correlation between the number of times a female clam spawns and the number of eggs produced was not significantly different from zero.

LITERATURE CITED

- BELDING, D. L., 1912. The quahaug fishery of Massachusetts. The Comm. of Mass. Dept. of Conserv. Marine Fisheries, Series No. 2: 1-41.
- BROOKS, W. K., 1880. The development of the oyster. Cont. Chesapeake Zool. Lab. Johns Hopkins Univ., No. IV: 1-115.
- BURKENROAD, M.D., 1947. Egg number is a matter of interest in fishery biology. Science, 106: 290.
- CHURCHILL, E. P., JR., 1920. The oyster and the oyster industry of the Atlantic and Gulf States. Bur. Fish. Doc., No. 890: 5-51.
- GALTSOFF, P. S., 1930. The fecundity of the oyster. Science, 72: 97-98.

GALTSOFF, P. S., 1938. Physiology of reproduction of Ostrea virginica. II. Stimulation of spawning in the female oyster. Biol. Bull., 75: 286-307.

GALTSOFF, P. S., 1940. Physiology of reproduction of Ostrea virginica. III. Stimulation of spawning in the male oyster. Biol. Bull., 78: 117-135.

- LOOSANOFF, V. L., 1937. Seasonal gonadal changes of adult clams, Venus mercenaria (L.). Biol. Bull., 72: 406-416.
- LOOSANOFF, V. L., AND H. C. DAVIS, 1950. Conditioning V. mercenaria for spawning in winter and breeding its larvae in the laboratory. Biol. Bull., 98: 60-65.

LOOSANOFF, V. L., AND C. A. NOMEJKO, 1951. Spawning and setting of the American oyster, O. virginica, in relation to lunar phases. Ecology, **32**: 113-134.

NELSON, T. C., 1921. Aids to successful oyster culture. N. J. Agric. Exp. Sta. Bull., 351: 7-59.